PINE HILLS ELYMUS

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The wide variation from stout filaments to mere stubs in the glume structure of occasional populations of *Elymus Hystrix* L. strongly suggests that the origin may lie in the hybridization and introgression of the common glumeless forms with some other species of *Elymus* possessing well-developed glumes (Church 1967). In fact, experimental hybrids between *E. Hystrix* and *E. canadensis* L. var. *canadensis*, although sterile, exhibit spikes with abundant and setaceous glumes, intermediate between those of the parents. Also noteworthy is the fact that the same strain of glumeless *E. Hystrix* has been crossed with *E. Svensonii* Church, an endemic Tennessee species with long, setaceous glumes, to produce a partly fertile F_2. *Elymus Svensonii* in turn was crossed with *E. virginicus* L. var. *glabriflorus* (Vasey) Bush f. *glabriflorus*, a common form with relatively broad glumes in southeastern United States, to produce a vigorous, intermediate and segregating F_2 (Church 1967). Hence it seemed reasonable to expect that in habitats where *E. Hystrix* and f. *glabriflorus* were sympatric, natural hybridization might give rise to partly fertile plants variously intermediate between the parents.

An appropriate location in which to study hybridization of these two taxa was found on the limestone bluffs immediately adjacent to the Mississippi River drainage area near La Rue, Union County, Illinois. Fortunately, the area is maintained as a wildlife reservation by the University of Southern Illinois and through the kindness of Professor J. W. Voigt, the author was able to locate the station where collections of *Elymus* with setaceous glumes had been made. Here one may find *E. Hystrix* and abundant stands of *E. virginicus* that exhibit considerable variation in glume

structure, and these populations constitute the major part of the present study.[1]

A diagram of the Pine Hills area, based on a tracing of the geological survey map of the region (Alto Pass Quad. U.S.G.S.), is shown in figure 1. In the upper section, the bluff of Devonian, sandy limestone rises a sheer 500 feet in places on the west side, as indicated by the contour lines. Immediately adjacent is a low, springy marsh through which the Big Muddy River (left middle) cuts through to the Mississippi River (lower left). The heavy line at the lower right represents Illinois Route 3, from which a dirt road leads eastward across a ditch and old railroad bed to the foot of the bluff. At this point the path continues through mixed, dense woodland northward, skirting the bluff, before it turns westward (upper left) and rises from the moist, shady low area to the dry wooded crest. Here the forest dominants include the Post Oak (*Quercus stellata* Wang.), Black Hickory (*Carya buckleyi* Sarg.), and Red Cedar (*Juniperus virginiana* L. var. *crebra* Fern. and Grisc.) particularly on the edges of dry, hilltop prairies. The name of the locality, however, stems from the rare stands of the southern Shortleaf Pine (*Pinus echinata* Mill.) just back from the bluff edges (Mohlenbrock and Voigt 1959, Voigt and Mohlenbrock 1964).

The *Elymus* populations are confined largely to the edges of woodlands all along the path as is indicated in figure 1. From the author's observations during two collecting trips in 1960 and 1961, *E. Hystrix* is confined largely to the shady moist woodlands at the swamp level of the trail, with occasional stands at the beginning of the higher and drier woodlands (upper left, fig. 1, "Government Rock", under one mile scale). Scattered along the lower trail but much more abundantly on the upper dry bluff area are stands of *E.*

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virginicus var. *glabriflorus* which is readily distinguished from other varieties by longer glumes, longer lemma awns and well-exserted spikes (Fernald 1933). It is distinguished also from *E. canadensis* L. var. *canadensis*, with which it could be confused, by the indurated, non-striated bases of the occasionally bowed glumes, the shorter, obtuse (rather than clearly bi-dentate) tipped paleas and the very erect spikes.

One variant of var. *glabriflorus* has scabridulous glumes and lemmas: it is forma *glabriflorus* and will often be referred to in the remainder of this paper as f. *glabriflorus*. The other variant of var. *glabriflorus* has densely hirsute glumes and lemmas: it is forma *australis* and will often be referred to as *f. australis*. Both taxa grow in close association (figs. 1, 3, 4).

Quite unique among all *Elymus* at Pine Hills are populations with very setaceous glumes that appear to be natural hybrids of *E. Hystrix* and either f. *glabriflorus* or f. *australis* (fig. 4). The glume structure has, in fact, been the basis of former identification of these stands as representatives of *E. canadensis* L. var. *interruptus* (Buckl.) Church, a very different taxon (Mohlenbrock and Voigt 1959, Church 1967). These putative hybrids lie in greatest concentration at the first part of the path along the dry bluff just above the moist basal section (fig. 1). The locality would appear to be an area where *E. Hystrix* and *E. virginicus* come into contact. Here the cut and scraped margins of woodland paths offer a disturbed and therefore favorable habitat for the spread of hybrids between these parents.

THE NATURAL HYBRIDS

A study of the variable populations with respect to spikelet structure, cytology of meiosis of the pollen-mother-cells and fertility, measured by percentage of mature seeds, has presented two basic types: — *a*, those with glabrous lemmas, represented by 2670[2] (fig. 4) and *b*, those with

[2]Numbers refer to the author's collections in the Brown University Herbarium.

hirsute lemmas 2662 (fig. 4). As the diagram in figure 1 indicates, the putative hybrids are closely associated with either f. *glabriflorus* or f. *australis;* 2652, 2613 respectively (fig. 4).

Within group *a,* some populations have glumes that are heavily indurated and bowed at the base but taper to a setaceous awn and in these features resemble f. *glabriflorus,* 2595 (fig. 7). The longer (8 mm.) paleas, with truncate apices, however, suggest an *E. Hystrix* relationship. Based on a normal average of two seeds per spikelet, only 4% seed is formed. Much more frequent are forms (2668, 2670, figs. 2 and 4) with setaceous glumes, 0.2-0.5 mm. wide and pairs unequal in length, 12-15 or 18-30 mm. long. The reduction of occasional glumes to stubs and the partly spreading spikelets again suggest an *E. Hystrix* parentage. The ciliate margins of the paleas, on the other hand, are characteristic of f. *glabriflorus.*

Examination of pollen-mother-cells (at least 50 in each stage) reveals chiasma frequencies of 1.73-1.92 (median 1.90), two or three bridges at first meiotic anaphase and extrusions in ca. 25% of the mature pollen. Seed set is ca. 50% (20-60%).

In addition to the hirsute lemmas, the *b* group of putative hybrids is characterized consistently by filiform glumes of various lengths and a pronounced, overall glaucous appearance, which is frequently a characteristic of *E. Hystrix,* (2669 — fig. 6). Cytological irregularities are comparable in nature and frequency to those found in group *a,* with the exception of the appearance of 3-4 accessory chromosomes in the early stages of pollen-mother-cell meiosis.

Three specimens collected as living plants (2251, 2653, 2662) had seed sets of 0, 20, and 35%. It is significant that root-divided clones of these plants, grown in greenhouse pots and surrounded by closely grouped pots of *E. Hystrix* and f. *australis,* increased in seed set over three years as much as 80%. Evidence, then, for the possible origin of new forms by introgressive hybridization is rather convincing.

The following study is an attempt to demonstrate the ancestry of the hybrids by experimental crosses between the putative parents.

EXPERIMENTAL HYBRIDS

1. *E. Hystrix* crossed with *E. virginicus* var. *glabriflorus* f. *glabriflorus*

Sympatric crosses. A cross of 2669 *(E. Hystrix)* with pistillate 2652 (f. *glabriflorus*) produced a single intermediate F_1 plant (1:3:220),[3] (fig. 5). The F_2 (17:17)[4] segregated to give 15 fertile plants resembling f. *glabriflorus* and 2 intermediates resembling the F_1. One of the intermediates was sterile and the other 30% fertile. The latter had culms 60 cm. tall compared to parental culms of 100 cm., spikes 6 cm. long compared to 10-12 cm., glume width 1 mm. compared to the extremes of lacking or 1.5 mm. in the parents. The ratio of lemma body to awn length was 1:4 as in *E. Hystrix* compared to that of 1:3 in f. *glabriflorus.*

The essentially reciprocal cross (5:5:43) (fig. 6) resulted in an F_1 characterized by more setaceous (0.3 mm. wide) glumes, unequal in length and with indurated bases. These plants resembled rather closely natural hybrids such as 2670 (fig. 4) but were sterile. Other crosses with the same strains were failures (0:110).

Allopatric crosses. A collection of 2368 *(E. Hystrix)* from Rice County, Minnesota, consisted of vigorous plants with frequent vestigial glumes on the spikes. Material grown from seed in the greenhouse, however, was quite free of glumes and was employed successfully in crosses with f. *glabriflorus* from Pine Hills (figs. 9 and 10).

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[3]Three numbers in ( ) indicate: — surviving seedlings: seeds planted: florets emasculated. Occasional numbers in [ ] indicate original numbers of seeds germinated as opposed to number of surviving plants.

[4]Two numbers in ( ) indicate: — plants obtained: F_1 seeds planted, unless otherwise specified, as in failure of original cross.

In the case of crosses employing 2607 (f. *glabriflorus*), one produced a single, sterile F_1 plant (1:1:64) but the other (fig. 9) (1:2:42) gave rise to a partly fertile, intermediate plant (glumes 0.4 mm. wide) that strongly resembled many of the wild, putative hybrids from Pine Hills (2670, fig. 4). The F_2 (8:60) consisted of 2 partly fertile plants like f. *glabriflorus* and 6 intermediates with filiform glumes. One of the latter plants produced seeds (20:224) from which 4 F_3 individuals arose; these have remained vegetative.

The number of progeny obtained (10:51:121) was even greater in another cross in which 2603 (f. *glabriflorus*) was used as the pistillate parent (fig. 10), this collection being substantially identical to 2607. Again, the F_1 strongly resembled wild forms (2670, fig. 4) except for a slightly higher frequency of stubs among the setaceous glumes of the experimental hybrids. Three of this F_1 were fertile, 4 were sterile and the rest failed after the seedling stage. The survivors were ca. 15% fertile compared to 55% for the parents growing under the same greenhouse conditions.

Studies of the pollen-mother-cells revealed an average chiasma frequency of 1.91 compared with 1.98 for the parents. Although one or two bridges occurred in 40% of the first meiotic anaphases, less than 5% of the pollen showed extruded chromatin in the cytoplasm.

The F_2 (18[24]:43:274) consisted of 3 sterile plants resembling f. *glabriflorus*, one partly fertile *E. Hystrix*, 6 seedlings that failed and 8 partly fertile intermediates that looked very much like the F_1.

The reciprocal of the preceding cross produced an F_1 (4[5]:20:162) that consisted of one sterile and 3 intermediates that were 25% fertile. The F_2 (14:20) of 10 plants have remained vegetative for 3 years. The other survivors were ca. 12% fertile and resembled *E. Hystrix* with filiform glumes.

2. *E. Hystrix* crossed with *E. virginicus* var. *glabriflorus* f. *australis*

Sympatric crosses. In attempts to reproduce the natural hybrids with hirsute lemmas (2662, fig. 4), 2669 *(E. Hystrix)* was crossed with three morphologically identical strains 2613, 2647 and 2648 (all f. *australis*) with no success (0:110, reciprocal 0:77).

Allopatric crosses. The seeds of a cross of 2647 (f. *australis*) from Pine Hills with 2368 *(E. Hystrix)* from Minnesota failed to germinate (0:4:60). A similar failure resulted from a cross of the same 2647 with 2642 *(E. Hystrix)* from Michigan (0:5:56).

In the cross of pistillate 2669 *(E. Hystrix* from Pine Hills) with 2615 (f. *australis* from Tennessee) 3 plants were obtained (3:3:30). One of this F_1 remained vegetative, but the other two produced spikes that were glaucous like the pistillate parent but had hirsute lemmas inherited from the staminate parent. The long, setaceous glumes of irregular lengths gave these plants an appearance closely resembling some of the natural hybrids at Pine Hills 2662, fig. 4). After having remained sterile for 4 years, one of the spikes had a seed set of 18% which was apparently the result of selfing in this F_1.

Intermediate F_1 plants were also obtained when the same strain of *f. australis* from Tennessee was crossed with strains of *E. Hystrix* outside of Illinois. Pistillate 2615 (f. *australis*) crossed with 2643 (*E. Hystrix* from Michigan) resulted in 8 vigorous, intermediate F_1 plants (8:12:214), only one of which was fertile (2%).

The cross of pistillate 2369 *(E. Hystrix* from Wisconsin) with 2615 (f. *australis*) produced even more vigorous F_1 plants (3:5:18). These intermediates were sterile during the first year. In the second year, 19 spikes of this same F_1 were bagged and 24 seeds were harvested from 2578 florets. Ten F_2 plants were obtained (10:24). Although they were considerably less vigorous than the F_1, they exhibited a wide range of combinations of glume structure and lemma surface. Some plants resembled *E. Hystrix* in having no glumes but the lemmas were very hirsute. Several resembled the natural hybrids with hirsute lemmas from Pine

Hills mentioned above. All F_2 plants were sterile except one that was bagged and yielded 2 seeds in 480 florets.

3. *E. Hystrix* crossed with *E. virginicus* var. *virginicus*

Since the Pine Hills population 2600 (var. *virginicus*, fig. 3) with wide, indurated glumes and included spikes did not appear to play a direct role in the origin of the hybrid forms under study, only a few attempts at crossing with sympatric *E. Hystrix* were made and all of these were failures.

Among a series of unsuccessful allopatric crosses, the hybrid obtained by pollinating 2614 (var. *virginicus*) from Tennessee with 2642 *(E. Hystrix)* from Michigan yielded one fertile intermediate plant (1:1:72). Six surviving F_2 plants exhibited a variety of glume structures from setaceous to moderately wide and striated. The setaceous glume forms had a seed set of 10% compared with ca. 100% for the parents. One F_2 plant closely resembled *E. Hystrix* with occasional filiform glumes and was quite fertile.

4. Natural Hybrid *E. Hystrix* × *E. virginicus* f. *glabriflorus* crossed with f. *glabriflorus*

A representative of the natural hybrid population 2668 is shown in figures 2 and 8. It has a spike 20 cm. long, spreading spikelets and setaceous (0.2-0.3 mm. wide) glumes of unequal lengths. Sympatric crosses employing 2659 (f. *glabriflorus*) pollen were made, but the seedlings obtained all died at an early stage (0[9]:31:131). One cross (fig. 8), however, was particularly successful (12:16:63). This F_1 was intermediate between the parents and ca. 50% fertile. In comparison the parents were 10% (2668) and 90% (2659). The F_2 (12:42) segregated to give 4 fertile plants resembling 2668, 3 partly fertile plants resembling f. *glabriflorus* and 5 intermediate forms closely resembling the F_1 (fig. 8). These F_2 intermediates had an average seed set of 60% (with a range of 0-90%).

The reciprocal cross with the same 2668 and 2663 (f.

glabriflorus, similar to 2659) produced 2 intermediate F_1 plants (2:3:54) (fig. 2). One of these intermediates produced a single seed that gave rise to a partly fertile F_2 which resembled f. *glabriflorus* except for a glaucous appearance like that of the staminate 2668 (natural hybrid).

The data seem to indicate strongly, then, that 2668 is a hybrid and the experimental crosses with f. *glabriflorus* represent backcrosses with one of its parents. No allopatric crosses were made.

5. Natural Hybrid *E. Hystrix* × *E. virginicus* f. *australis* crossed with *E. Hystrix*

Sympatric crosses. A cross of pistillate 2657 (Natural Hybrid from Pine Hills) and 2669 *(E. Hystrix)* was a failure (0:50). However, the reciprocal cross gave a single, intermediate plant (1:3:59). Whereas the parental strain of the Natural Hybrid had setaceous glumes (0.2 mm. wide) with frequent striations, the F_1 plant had mostly filamentous, non-striated glumes and was strikingly fertile (40 seeds from 104 florets). The surviving F_2 of 38 plants has flourished in greenhouse pots for 3 years and has increased in fertility (as measured by seed set on 25 spikes) from 22-39%. The glumes of this F_2 are practically all filamentous from an indurated base or occasionally reduced to stubs and very rarely marked by a fine striation. This experimentally produced hybrid population had an even greater resemblance to strains of *E. Hystrix* with variable glume structure than did the parental strain 2657 (Natural Hybrid).

Allopatric crosses. Another strain 2653 (Natural Hybrid) was pollinated with 2643 *(E. Hystrix)* from Michigan with even greater success (10:28:67) than in sympatric crosses. The 2643 parent had quite glabrous lemmas and no glumes. The F_1 in this experimental cross had glumes more reduced and setaceous than those of the Natural Hybrid 2653. In the F_2 (38:90), 22 of the plants remained vegetative and the rest were intermediate in appearance like the F_1. Only 3 seeds arose in the F_2.

6. Natural Hybrid *E. Hystrix* × *E. virginicus* f. *australis* crossed with f. *glabriflorus*

Allopatric cross. In a cross of pistillate 2694 (f. *glabriflorus* from North Carolina) with 2651 (Natural Hybrid from Pine Hills), an F_1 of 2 plants was obtained (2:3:116). One of these had glumes approaching those of f. *glabriflorus* in width, hirsute lemmas like the Natural Hybrid and was sterile. The other plant had hirsute lemmas but setaceous glumes and a seed set that increased from 10% to 35% in the same potted individual after 4 years. The F_2 of 10 plants (10:18) exhibited considerable variation in glume structure but very few seeds. A reciprocal cross (2:9:45) had glumes intermediate between those of the parents but was quite sterile.

7. Experimental intervarietal hybrids of *E. virginicus*

Reciprocal crosses of 2600 (var. *virginicus* from Pine Hills) and sympatric 2663 (f. *glabriflorus*) failed (0:11:60 and (0:8:58). Reciprocal crosses of 2600 (var. *virginicus*) and allopatric 2615 (f. *australis* from Tennessee) did not even produce any seeds (0:64 and 0:90). As far as this limited data are concerned, these forms of *E. virginicus* appear genetically isolated from var. *virginicus*.

The question to arise next is the degree of isolation between f. *glabriflorus* and f. *australis*. After several failures, a cross of 2609 (f. *glabriflorus*) pistillate from Pine Hills and sympatric 2613 (f. *australis*) resulted in a single plant (1[8]:8:34). This F_1 individual had a seed set of 17% compared with parental yields of 53% pistillate and 49% staminate. Two F_2 survived (2:17). They had hirsute lemmas and were fertile. In the reciprocal cross with 2613 (f. *australis*) as the pistillate parent, 4 F_1 plants were obtained (4[10]:17:131). In contrast to the overall hirsute appearance of the spike in f. *australis*, these F_1 individuals were hirtellous only on the lemmas and were 20% fertile. The F_2 (0:18) was a failure.

In a cross of 2648 (f. *australis* from Pine Hills) with allopatric 2688 (f. *glabriflorus* from Virginia) as the pistillate parent a rather high percentage of seed was obtained (10:18:27). These F_1 plants were hirsute like f. *australis* but were stunted and sterile.

8. Crosses of *E. canadensis* L. var. *canadensis* with sympatric *E. virginicus* f. *australis*

Since *E. canadensis* var. *canadensis* is known to cross fairly readily with strains of *E. virginicus* in other areas (Church 1958, 1967), it was thought appropriate to test the degree of genetic isolation between representatives of these taxa at Pine Hills. A cross of 2611 (var. *canadensis*, fig. 3) with staminate 2597 (f. *australis*) produced 8 seedlings that died at an early stage of development (0:8:82). The reciprocal cross failed. Although these data are limited, genetic barriers between these taxa appear strong.

CONCLUSIONS AND SUMMARY

Examination of Chart A presents a summary of the results of the experimental crosses of *Elymus* species as they relate primarily to the origin of the Pine Hills, Illinois hybrid populations of *E. Hystrix* crossed with sympatric *E. virginicus f. glabriflorus* or f. *australis*. Chart B indicates the genetic compatibility of these parents and their hybrids from selected areas of their range in eastern United States.

Natural Hybrid *E. Hystrix* × *E. virginicus* f. *glabriflorus*

The data presented indicate clearly that the origin of forms of *E. virginicus* with setaceous glumes and glabrous lemmas lies in natural hybridization between *E. Hystrix* and *E. virginicus* f. *glabriflorus*. In sympatric parental populations (Chart A), barriers to hybridity are quite strong as is evident from the high percentage of failures or sterility in the F_1. Since, however, partly fertile intermediates resembling natural hybrids appear in the F_2

from even a single F_1 plant, the origin of natural hybrids is demonstrated. Although similar barriers to crossing are encountered when allopatric *E. Hystrix* is employed, (Chart B) partly fertile forms similar to the natural hybrids have appeared in both the F_1 and F_2. Again the parents of the wild hybrids are identified.

In a series of the allopatric crosses of *E. Hystrix* with f. *glabriflorus*, it is noteworthy that in over half of the cases sterility was not encountered until the F_2 was fully developed. Probably related to these results is the fact that out of 10 inter-strain allopatric crosses of f. *glabriflorus*, only 5 gave offspring with seed set over 60%. The implied existence of genes that make for intra-specific incompatibility might also explain the lack of uniform results in all allopatric crosses of *E. Hystrix* with f. *glabriflorus*.

Of particular significance is the fact that the natural hybrids cross readily with sympatric f. *glabriflorus* (Chart A), and the offspring are still intermediate in appearance but with a much higher average of wider (0.5 mm. rather than 0.2 mm.) glumes and fewer reduced stubs than appear in the natural hybrid parent. The seed set of 25% would seem to be sufficient to maintain such back-crossed or introgressed (*E. Hystrix* into f. *glabriflorus*) populations under field conditions and thereby establish the basis for the evolution of a new taxon through further back-crossing and attendant increased fertility.

Natural Hybrid *E. Hystrix* × *E. virginicus* f. *australis*

It has been more difficult to produce the type *b* (hirsute lemmas) natural hybrids than in the case of type *a* (glabrous lemmas). Although the *b* type hybrids are encountered frequently at Pine Hills, barriers to crossing between the sympatric *E. Hystrix* and f. *australis* populations are very strong. However, experimental partly fertile hybrids, closely resembling the natural hybrids were obtained in the F_1 in the case where the f. *australis* parent came from Tennessee (Charts A and B).

Furthermore, the fact that partly fertile hybrids similar to those at Pine Hills appeared in the F_2 of experimental crosses in which neither parent came from Illinois, certainly is indicative of significant genetic compatibility between these taxa in broad segments of their ranges.

Finally, the fact that the experimental crosses of the natural hybrids to either sympatric or allopatric *E. Hystrix* resulted in F_2 plants resembling the parental natural hybrids but with increased fertility, is strong evidence of the ability of the natural hybrids to become the basis of new taxa under field conditions as in the case of the type *a* hybrids considered above.

The varieties of *E. virginicus*

Since the major effort of the program of experimental hybridization has focused on *E. Hystrix*, the data pertaining to the varieties of *E. virginicus* per se are rather limited. However, there would appear to be definite genetic barriers between f. *glabriflorus* and f. *australis* in all cases reported (Charts A and B), although in one instance these were not reached until the F_2. In spite of the fact that f. *australis* appears as merely a robust, hirsute variant of *E. glabriflorus* var. *glabriflorus*, studies so far show strong genetic isolation from not only f. *glabriflorus* (Chart A) but also from the common var. *virginicus* (Chart B).

The evolutionary status of *E. Hystrix*

In the large number of inter-generic hybrids, natural or artificial, that have been reported in the Hordeae tribe of the Gramineae, all are sterile (Church 1967). In contrast, the many experimental hybrids involving *E. Hystrix* in these studies maintain at least partial fertility in the F_2. It seems unjustifiable, therefore, to maintain this species in a separate genus (*Hystrix patula* Moench).

As previously noted, many of the segregates of experimental crosses of *E. Hystrix* with *E. virginicus* f. *glabriflorus* are intermediate in glume structure between the parents. It should be noted further that these hybrids vary in spikelet structure: the majority have spikelets of several

florets more or less adherent to the rachis but others have spreading spikelets of few florets. These latter segregates resemble *E. Hystrix* except for the abundant filiform glumes. Such "glumed forms" of *E. Hystrix* are encountered in many parts of the range of the species (Church 1967). Samples of such a population from North Carolina (2698) have been observed to breed essentially true from seed with varying percentages of seed set in the progeny of the two generations studied. In general, the spikes have an appearance suggesting introgression from f. *glabriflorus* into *E. Hystrix* rather than the reverse pattern of gene flow that is indicated in the Pine Hills natural hybrids. Both of the putative parents lie well within the range of populations like 2698 in both North and South Carolina, and it is possible that hybrids intermediate between *E. Hystrix* and *E. virginicus* var. *glabriflorus* have arisen in this eastern part of their range as they have in Pine Hills.

It is conceivable, on the other hand, that populations of *E. Hystrix* with glumes represent a primitive condition of the species, in which case the glumeless condition might be the result of subsequently established mutations occurring in populations ecologically isolated from other *Elymus* species. Possibly the glumeless condition is basically homozygous recessive, since in a cross of *E. virginicus* f. *glabriflorus* with staminate *E. Hystrix*, only one of 20 F_2 plants was identical to *E. Hystrix* with glumes entirely missing in addition to being 50% fertile.

The strikingly different overall appearance between *E. Hystrix* and *E. virginicus* var. *glabriflorus* f. *glabriflorus* (or f. *australis*) masks their strong genetic affinity. However, a parallel case within the genus is presented by the facility with which strains of *E. virginicus* var. *virginicus* and the very different appearing *E. canadensis* var. *canadensis* will cross in some instances to produce F_1 populations, some of which are slightly fertile (Brown and Pratt 1960, Church 1958, Pohl 1959).

In relation to *E. Hystrix* attention is directed also to *E. californicus* Gould, an endemic of the San Francisco

area, which was formerly placed in the genus *Hystrix* (Gould 1947). The somatic chromosome number of 56 (Stebbins, G. L. in Myers, E. M. 1947) would indicate that this species is octoploid in contrast to the somatic complement of 28 for *E. Hystrix*. The author has succeeded in raising a few plants of *E. californicus* in the greenhouse at Brown University but in two growing seasons they have not reached maturity and, therefore, crossing experiments between these two species remain for future study.

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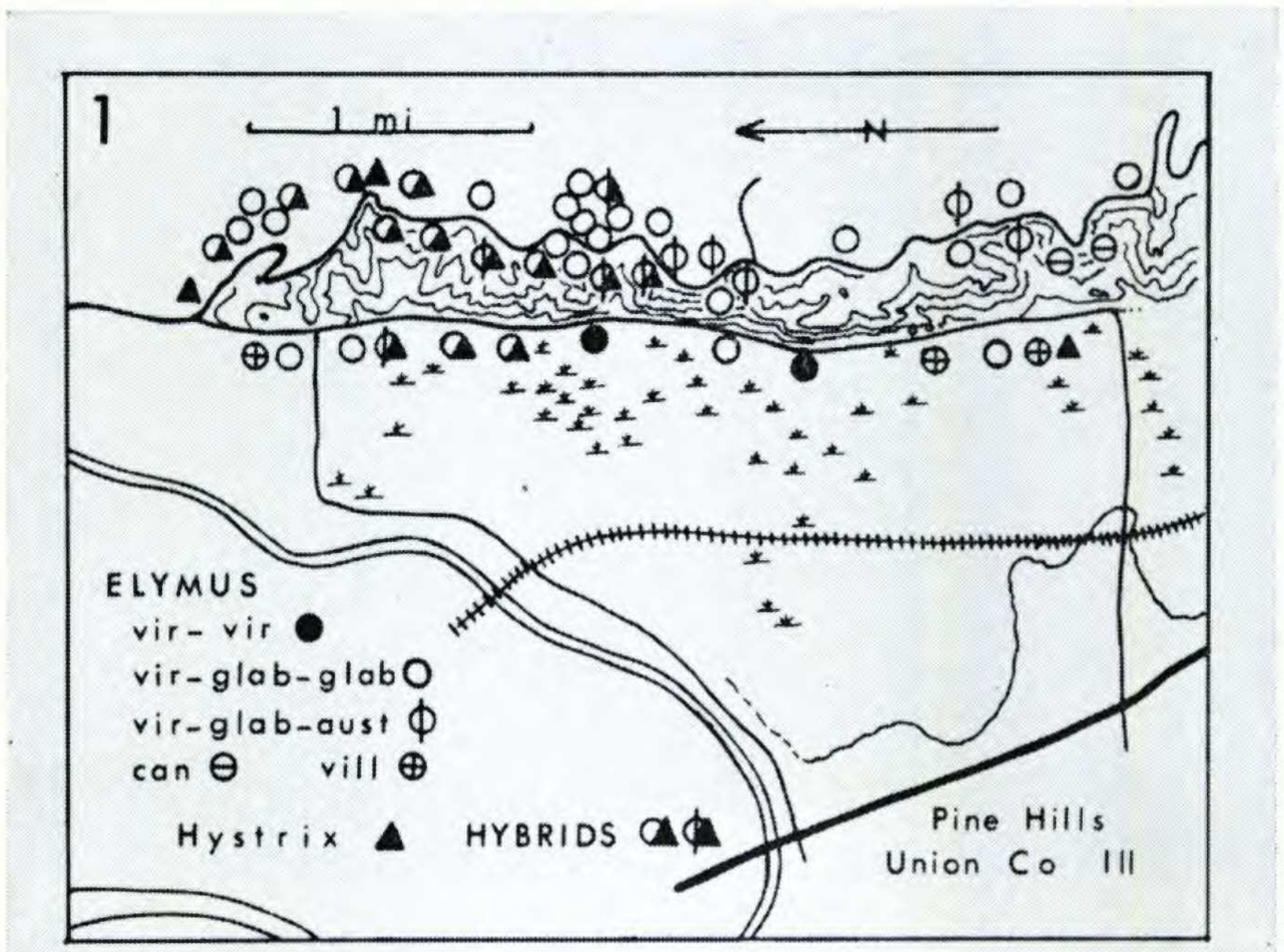

Fig. 1. Topographic diagram of the Pine Hills area showing distribution of parental and hybrid species of *Elymus:* see text for explanation.

Fig. 2. left to right — *E. virginicus* f. *glabriflorus* 2663; experimental F_1; natural hybrid of *E. Hystrix* × *E. virginicus* f. *glabriflorus* 2668.

Fig. 3. left to right — *E. canadensis* var. *canadensis* 2611; *E. virginicus* var. *virginicus* 2600; *E. virginicus* f. *glabriflorus* 2652; *E. villosus* 2685.

Fig. 4. left to right — *E. virginicus* f. *glabriflorus* 2652; natural hybrid *E. Hystrix* × *E. virgincus* f. *glabriflorus* 2670; natural hybrid *E. Hystrix* × *E. virginicus* f. *australis* 2662; *E. virginicus* f. *australis* 2613.

Fig. 5. experimental F_1 of *E. virginicus* f. *glabriflorus* 2652 (pistillate) × *E. Hystrix* 2669.

Fig. 6. left to right — E. *Hystrix* 2669 (pistillate — one spikelet removed at each node for clarity); experimental F_1; *E. virginicus* f. *glabriflorus* 2656 (staminate).

Fig. 7. natural hybrid *E. virginicus* f. *glabriflorus* × *E. Hystrix* 2595.

Fig. 8. left to right — natural hybrid *E. Hystrix* × *E. virginicus* f. *glabriflorus* 2668 (pistillate — some spikelets removed); experimental hybrid (probable backcross); *E. virginicus* f. *glabriflorus* 2659 (staminate).

Plate 1361.

Fig. 9. left to right — *E. Hystrix* 2368 (pistillate, some spikelets removed); experimental F_1 hybrid; *E. virginicus* f. *glabriflorus* 2607 (staminate).

Fig. 10. left to right — *E. virginicus* f. *glabriflorus* 2603 (pistillate); experimental F_1 hybrid; *E. Hystrix* 2368 (staminate — some spikelets removed).

SYMPATRIC CROSSES

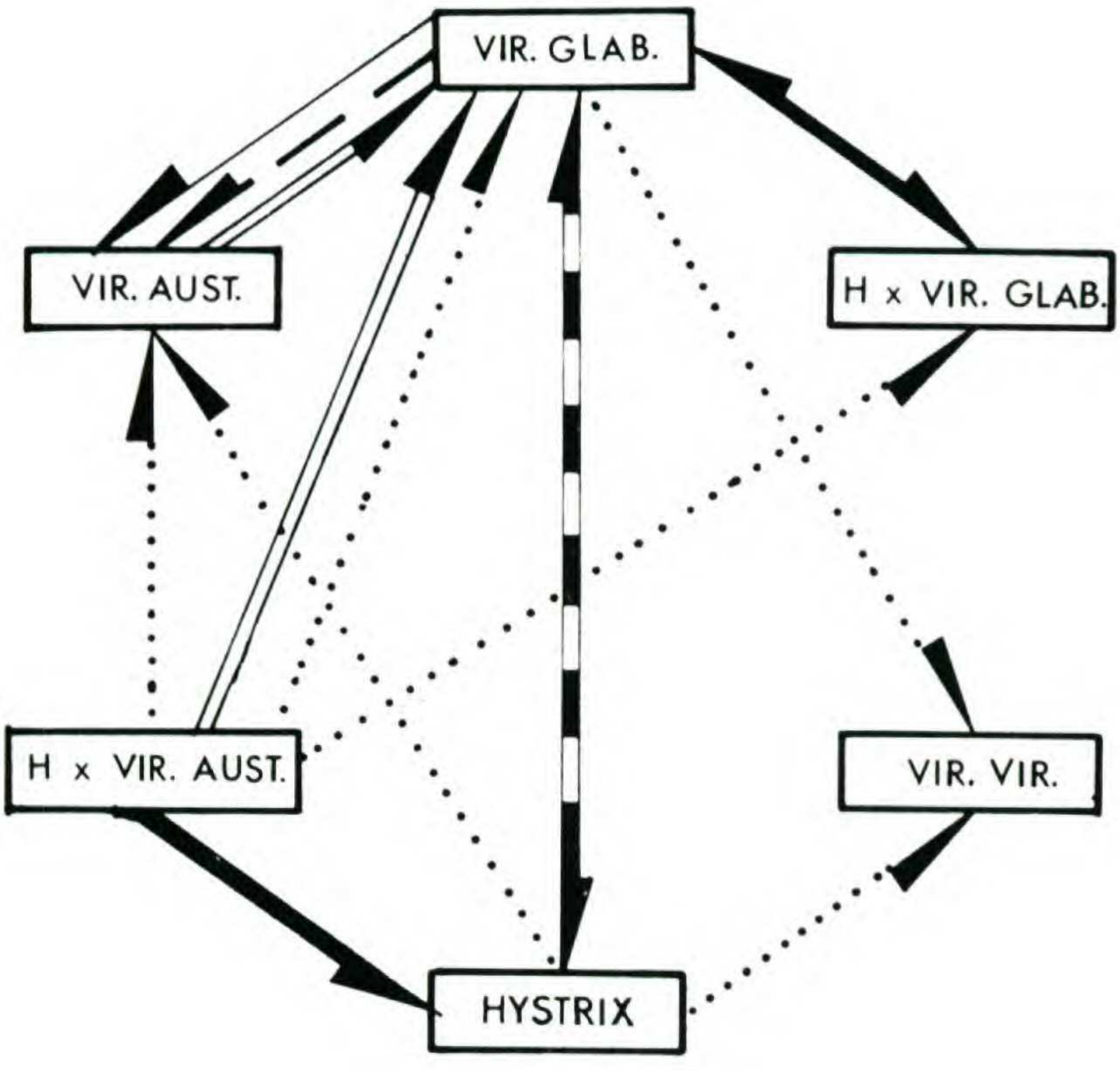

Chart A

ALLOPATRIC CROSSES

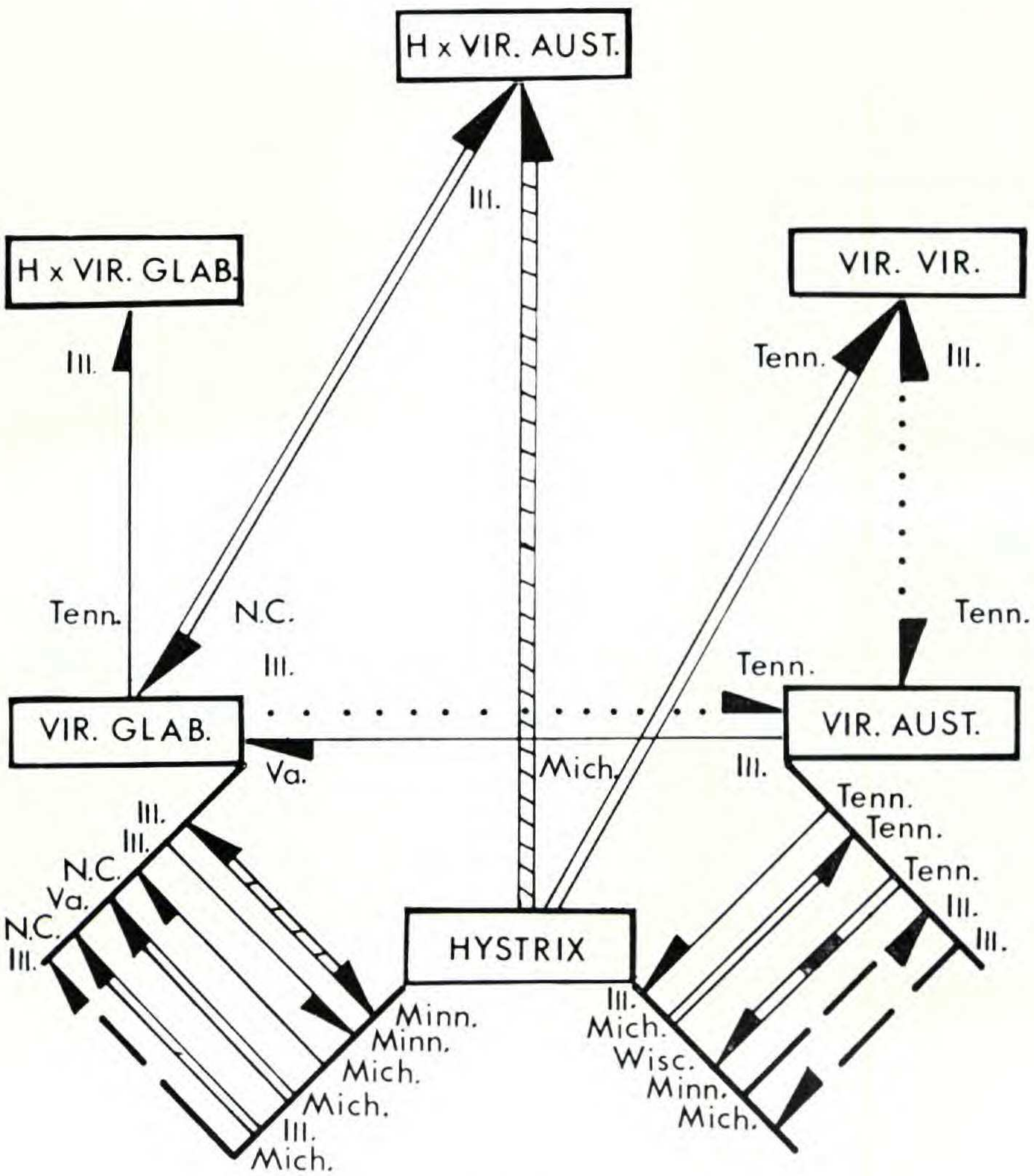

Chart B

HYSTRIX — *Elymus Hystrix*
VIR VIR — *Elymus virginicus* var. *virginicus*
VIR GLAB — *Elymus virginicus* var. *glabriflorus* f. *glabriflorus*
VIR AUST — *Elymus virginicus* var. *glabriflorus* f. *australis*
H × VIR GLAB — Natural Hybrid between *Elymus Hystrix* and *E. virginicus f. glabriflorus*
H × VIR AUST — Natural Hybrid between *Elymus Hystrix* and *E. virginicus* f. *australis*